

EXCEPTIONAL NEW DENTITIONS OF THE DIMINUTIVE  
PLESIADAPIFORMS *TINIMOMYS* AND *NIPTOMOMYS* (MAMMALIA),  
WITH COMMENTS ON THE UPPER INCISORS OF  
PLESIADAPIFORMES

KENNETH D. ROSE<sup>1</sup>

Research Associate, Section of Vertebrate Paleontology

K. CHRISTOPHER BEARD

Associate Curator, Section of Vertebrate Paleontology

PETER HOUDE<sup>2</sup>

ABSTRACT

Complete lower and nearly complete upper dentitions of the micromomyid *Tinimomys graybulliensis* and a nearly complete lower dentition of the microsyopid *Niptomomys doreenae* are illustrated, and previously unknown teeth are described. Both specimens are from the lower Willwood Formation (early Wasatchian) of the Bighorn Basin, Wyoming. The first known I<sup>1-2</sup> of *T. graybulliensis* provides the stimulus for broader comparison of the specialized upper central incisors of plesiadapiforms. Plesiadapids, paromomyids, saxonellids, and carpolestids have more or less similar, multicusped I's, supporting close relationship of these families. I<sup>1</sup> structure suggests that micromomyids are more distantly related (although postcranial evidence suggests that they may be closer to Paromomyidae). None of these plesiadapiform upper incisors shows any particular resemblance to those of euprimates. Based on incisor form, Microsyopidae are likely to be only distantly related to plesiadapiforms.

INTRODUCTION

The Clarkforkian-early Wasatchian plesiadapiforms *Tinimomys graybulliensis* and *Niptomomys doreenae* are among the smallest species that have been referred to the Primates, each probably weighing less than 35 g (see Conroy, 1987; Fleagle, 1988; and below for body weight estimates). With molars on the order of 1 mm long, their cheek teeth are substantially smaller than those of any extant primate (cf. Swindler, 1976), rivalling those of shrews (cf. Repenning, 1967) in their diminutive size.

*Tinimomys* represents the family Micromomyidae, and *Niptomomys* belongs to the uintasoricine Microsyopidae. While these assignments are relatively well established, the precise phylogenetic position of both families within Plesiadapiformes, and even their allocation to this suborder, are uncertain. For example, Szalay and Delson (1979) included *Tinimomys* in the plesiadapiform family Paromomyidae, but excluded Microsyopidae (including *Niptomomys*) from Plesiadapiformes and Primates. Hoffstetter (1988) followed Szalay and Delson concerning Microsyopidae, and even questioned the plesiadapiform status of

<sup>1</sup> Department of Cell Biology & Anatomy, Johns Hopkins University School of Medicine, Baltimore, Maryland 21205.

<sup>2</sup> Department of Biology, New Mexico State University, Las Cruces, New Mexico 88003.  
Submitted 5 May 1993.

*Tinimomys*. Gunnell (1989), however, included both of these genera in the Microsyopidae, within the suborder Plesiadapiformes, which he retained in the Primates with a query.

The primate status of Plesiadapiformes as a whole also has been seriously questioned in recent years (e.g., Martin, 1986, 1990; Gingerich, 1989; Gunnell, 1989; Beard, 1990, 1991, 1993; Kay et al., 1990, 1992), although nearly all studies agree that they are closely related to undoubted primates. Beard (1990, 1991, 1993) presented postcranial and other evidence that most taxa conventionally included in Plesiadapiformes are closer to Dermoptera (otherwise consisting of only the extant *Cynocephalus*) than to Primates, and he expanded the Dermoptera to include these plesiadapiforms. He further proposed that Dermoptera is the probable sister group of Primates (i.e., Euprimates). Kay et al. (1990, 1992) documented cranial characters that support a close alliance between plesiadapiforms and Dermoptera, but their analysis led to the conclusion that Scandentia rather than Plesiadapiformes is the sister group of Primates.

Resolution of these controversies is obviously beyond the realm of this note. For convenience, however, we refer herein to *Tinimomys* and *Niptomomys* as plesiadapiforms.

Early Wasatchian specimens of the plesiadapiforms *Tinimomys graybulliensis* and *Niptomomys doreenae* recently discovered in the lower Willwood Formation of the Bighorn Basin, Wyoming, are the most complete known dentitions of these species and provide previously unknown information about the antemolar dentitions. Although both of these species have become better known in recent years (e.g., Bown, 1979; Rose and Bown, 1982; Beard and Houde, 1989; Gunnell, 1989), they are still among the rarest elements of early Eocene mammalian faunas. The purpose of this note is to put on record the anatomy of these exceptional new specimens which, in the case of *Tinimomys*, contributes new information bearing on its phylogenetic position.

Abbreviations are as follows: a, anterocone; l, laterocone; lc, lateroconule; m, mediocone; mc, mediocrista; p, posterocone. Institutional acronyms are: AMNH, American Museum of Natural History, New York; AV, Muséum National d'Histoire Naturelle, Paris; PAT, Laboratoire de Paléontologie, Montpellier, France; UA, University of Alberta, Edmonton; UM, University of Michigan, Ann Arbor; USGS, U.S. Geological Survey, Denver; USNM, National Museum of Natural History, Washington, D.C.; UW, University of Wyoming, Laramie; Wa, Geologisch-Paläontologisches Institut, Halle, Germany.

#### SYSTEMATIC PALEONTOLOGY

##### Family Microsyopidae Osborn and Wortman, 1892

##### *Niptomomys doreenae* McKenna, 1960

A nearly complete right dentary of this species (USGS 25496; Fig. 1) was collected in 1992 by Suzanne Strait from very low in the Willwood Formation (UW locality V-73037, approximately 5 miles east of Worland, Washakie County, Wyoming; 34-m level; see Bown, 1979). It preserves  $P_3$ - $M_3$ , the bases of two anterior teeth, and an alveolus between them and  $P_3$ . The two anterior teeth, the first enlarged and the second vestigial, have been interpreted as  $I_1$  and the canine, giving a lower dental formula of 1-1-3-3 (Bown and Gingerich, 1972). However, the close proximity and small size of the second tooth, and the slightly larger size of the third tooth (as suggested by its alveolus), leave open the possibility that



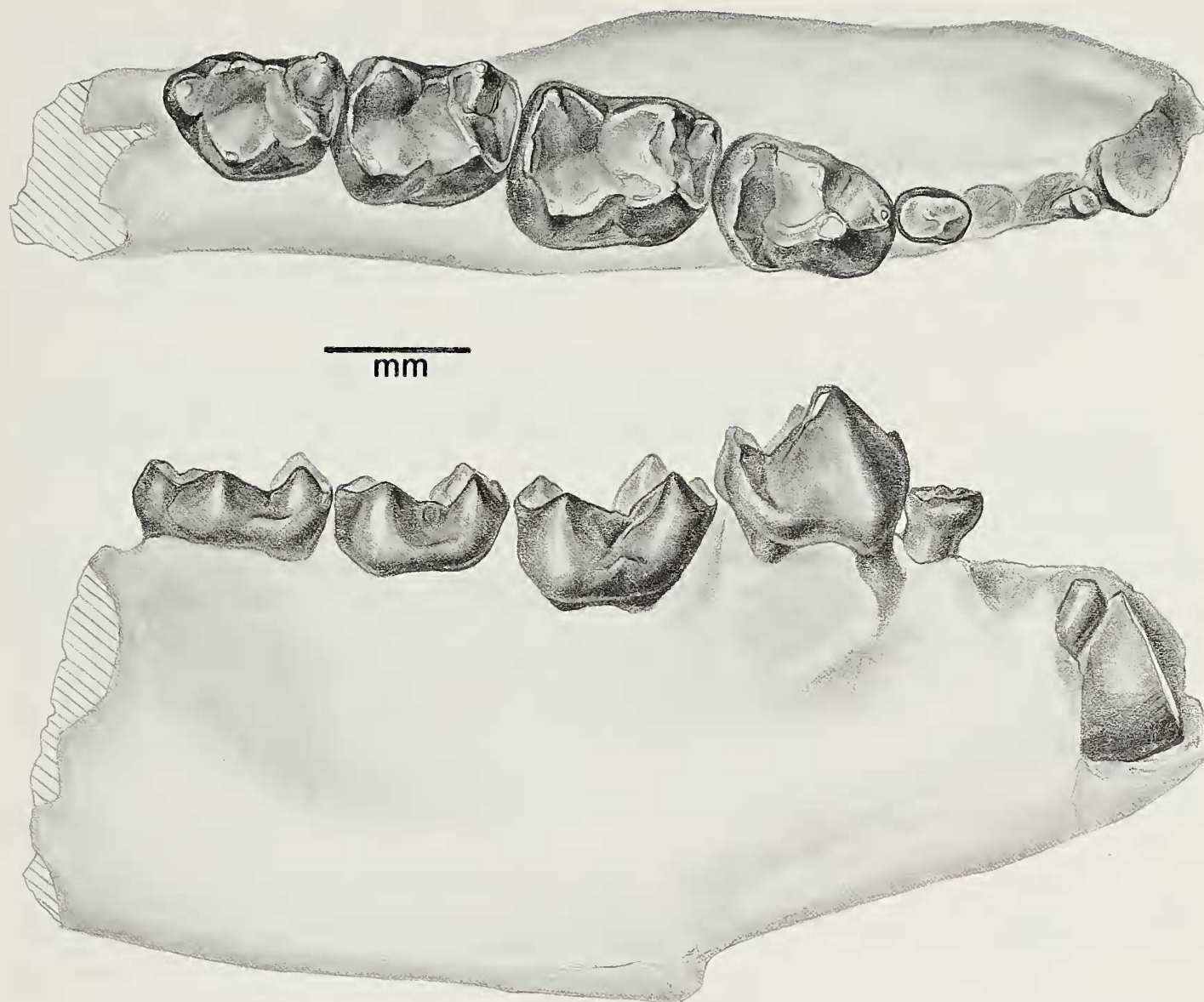


Fig. 1.—*Niptomomys doreenae*, USGS 25496, right dentary with  $P_3$ – $M_3$  and bases of  $I_1$  and ?C; occlusal and lateral views. Scale is 1 mm.

the lower dental formula could be 2-1-2-3 or even 2-0-3-3. The lower dentition of this species has been adequately described by McKenna (1960), Szalay (1969*b*), and Bown (1979).

Measurements (mm) of USGS 25496 are:  $P_3$  length = 0.5, breadth = 0.4;  $P_4$  L = 1.25, B = 0.95;  $M_1$  L = 1.35, B = 1.15;  $M_2$  L = 1.20, B = 1.00;  $M_3$  L = 1.25, B = 0.85.

Family Micromomyidae Szalay, 1974  
*Tinimomys graybulliensis* Szalay, 1974

Associated lower and upper dentitions (USNM 461201, Fig. 2) of this diminutive species were extracted by acid preparation from a nodule collected in the Willwood Formation of the Clark's Fork Basin, Wyoming (approximately UM locality SC-26, sec. 4, T. 55 N., R. 101 W., Park County, Wyoming; early Wasatchian; see Rose, 1981; Gingerich and Klitz, 1985; Houde and Olson, 1992). The right dentary is complete except for the top of the coronoid process, and contains its full complement of seven teeth. The lower dental formula has been interpreted to be 1-0-3-3 (Bown and Rose, 1976; Beard and Houde, 1989; Gunnell, 1989), but there is, in fact, little direct evidence for this interpretation and it could as well be 1-1-2-3, or even 2-0-2-3. A palatal fragment contains the right  $P^2$ – $M^3$ .

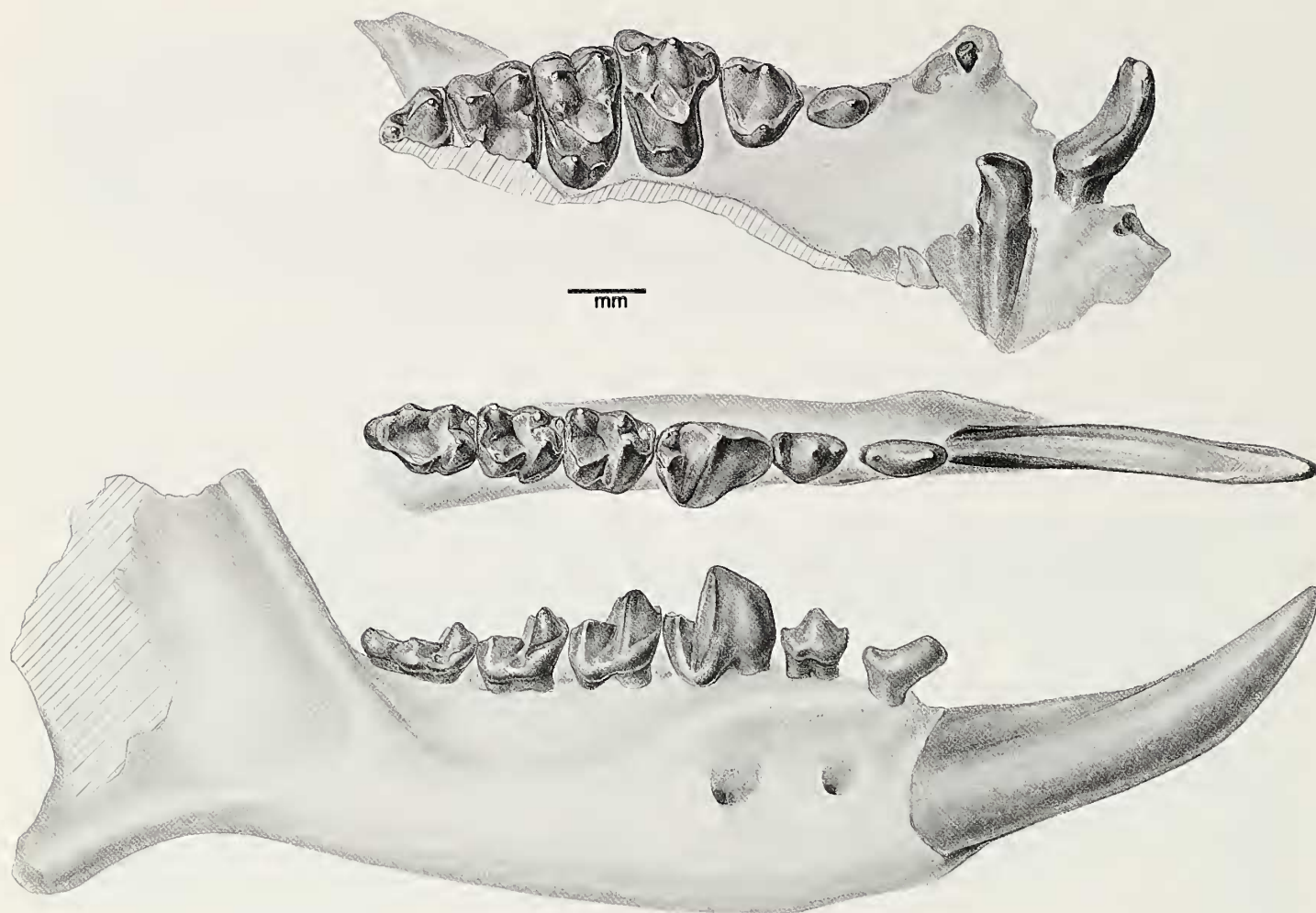


Fig. 2.—*Tinimomys graybulliensis*, USNM 461201. Top: Fragmentary palate with right P<sup>2</sup>–M<sup>3</sup> (M<sup>2-3</sup> incomplete lingually) and left I<sup>1-2</sup>. Center and bottom: Right dentary with complete dentition, in occlusal and lateral views. Scale is 1 mm.

Anterior to P<sup>2</sup> and separated by a short diastema are two alveoli (the anterior one containing a small root), evidently for a two-rooted canine or P<sup>1</sup>. Attached to the palate is a left premaxillary fragment with two incisors, which has been displaced posteriorly. The teeth are interpreted as I<sup>1-2</sup> because the anteriormost is larger and broader and has accessory cusps besides its apical cusp (as is typical of the central incisor in plesiadapiforms; a mesial contact facet cannot be discerned); whereas the second tooth is laterally compressed and simple, resembling I<sup>2</sup> in *Ignacius* and *Nannodectes*. Isolated right I<sup>1-2</sup> are also preserved.

P<sub>3</sub>–M<sub>3</sub> and P<sup>3</sup>–M<sup>3</sup> have been figured and described previously (e.g., Szalay, 1974; Bown and Rose, 1976; Gunnell, 1989; Beard and Houde, 1989). The elongate, laterally compressed lower incisor, as observed by Beard and Houde (1989), more closely resembles that of *Saxonella* than of any other plesiadapiform. The second tooth (P<sub>2</sub>?) has an elongate crown, which projects anteriorly over its single root. It is a simple tooth with a large anteriorly placed protoconid followed by a low talonid cusp. P<sup>2</sup> is also simple but two-rooted, longer than wide, and has an anteriorly situated apical cusp and a faint lingual cingulum. I<sup>2</sup> is simple, laterally compressed, with a slightly recurved tip. Its crown is about three-fourths as high as that of I<sup>1</sup>. The central incisor is robust at its base, about twice as deep labiolingually as it is in transverse diameter. In lateral profile the crown is hook-shaped. It is dominated by a large, somewhat laterally situated apical cusp (presumably homologous with the anterocone of plesiadapids) separated by a shallow furrow from a much smaller and lower medial cusp (mediocone). The basolingual border



of the right I<sup>1</sup> is faintly swollen in the position of a posterocone, but this can barely be discerned on left I<sup>1</sup>. Basolaterally is a weakly formed cusp here termed a *lateroconule* rather than a laterocone, because it is basal rather than apical; a true laterocone appears to be absent. Comparison of this distinctive I<sup>1</sup> with those of other plesiadapiforms affords new evidence on the affinities of *Tinimomys*.

Measurements (mm) of USNM 461201 are: P<sub>2</sub> or C length = 1.05, breadth = 0.50; P<sub>3</sub> L = 0.95, B = 0.65; P<sub>4</sub> L = 1.40, B = 1.10; M<sub>1</sub> L = 1.20, B = 1.10; M<sub>2</sub> L = 1.10, B = 0.95; M<sub>3</sub> L = 1.45, B = 0.90; P<sup>2</sup> L = 0.80, B = 0.50; P<sup>3</sup> L = 1.10, B = 1.15; P<sup>4</sup> L = 1.35, B = 1.80; M<sup>1</sup> L = 1.10, B = 1.70; M<sup>2</sup> L = 1.05.

#### UPPER INCISORS OF PLESIADAPIFORMS

The upper central incisors of many plesiadapiforms are easily recognized by their distinctive multipronged “mitten-shaped” crowns. Although this characteristic structure has long been known (e.g., Matthew, 1917; Gidley, 1923), surprisingly few specimens have been found that preserve serially associated upper incisors with complete crowns in the same jaw with cheek teeth; most upper incisors that have been allocated to various plesiadapiform species are isolated. Besides *Tinimomys* described here, serially associated upper central incisors have been illustrated or described only in the plesiadapids *Nannodectes* (Matthew, 1917; Simpson, 1935; Gingerich et al., 1983) and *Plesiadapis* (Russell, 1967; Gingerich, 1976), the carpolestid *Carpolestes* (Gingerich, 1987), the paromomyid *Arcius* (Godinot, 1984), and the microsyopids *Microsyops* (Gunnell, 1989) and *Megadelphus* (Szalay, 1969a; Gunnell, 1989)—and for only a single specimen of each except in the case of *Nannodectes* and *Arcius*, where there are two. Incisors have been reported for several other plesiadapiform genera, but taxonomic allocations have been based on presumed association, size, or morphology consistent with the incisors of taxa listed above, and they remain to be corroborated.

Incisors of various plesiadapiforms are illustrated in Fig. 3. It is evident that the incisors of plesiadapids (Fig. 3C), paromomyids (Fig. 3D–H), saxonellids (Fig. 3J), and carpolestids (Fig. 3K) are variations on a similar theme, and the probable specialized nature of this structure is further evidence of the close relationship among these plesiadapiform families. I<sup>1</sup> in members of all these families is characterized by a prominent anterocone (usually the largest cusp), a large laterocone, a variably developed mediocone (absent in at least some carpolestids and paromomyids), and a distinct posterocone (again of variable expression). The mediocone is situated more proximally in plesiadapids than in other plesiadapiforms (about even with the laterocone), and it is possible that not all mediocones are homologous.

Plesiadapid I<sup>1</sup>s (except *Platychoerops*, which was apparently further modified: Gingerich, 1976:fig. 26) always have the anterocone as the largest cusp, with the laterocone typically large as well, except in the most derived species in which the laterocone may be reduced (Gingerich, 1976; Krause, 1978:fig. 4, 10; Hooker, 1991:fig. 1). The posterocone is also well-developed, whereas the mediocone tends to be much smaller and lower than the anterocone. A weak centroconule is present between the mediocone and laterocone in some later species (e.g., *Plesiadapis rex*, *P. churchilli*, *P. tricuspis*: Gingerich, 1976; Krause, 1978). In *Nannodectes gidleyi* (Fig. 3C) there is a basolateral accessory cusp (termed here the lateroconule and in the same position as that of *Tinimomys*) between the laterocone and the base of the crown. A similar, possibly homologous cusp occurs in two other incisor morphs discussed below (Fig. 3B, 3L) as well as *Tinimomys*.



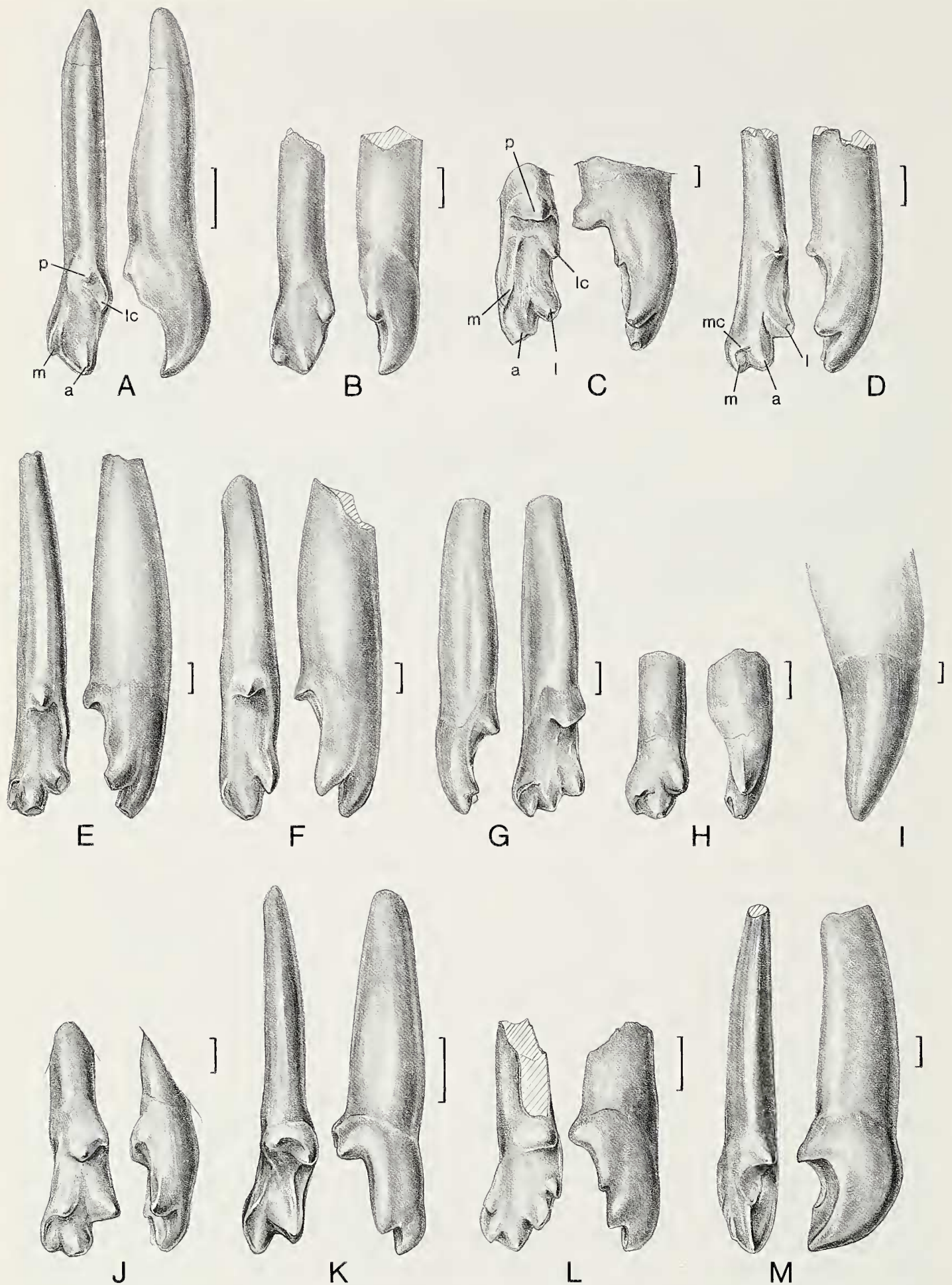


Fig. 3.—Right upper central incisors of plesiadapiforms and related forms, in lingual and lateral views unless otherwise noted. A, *Tinimomys graybulliensis*, USNM 461201; B, Unidentified left incisor (reversed), possibly *Palaechthon alticuspis*, USNM 10090, partly restored from USNM 10010 (Torrejonian); C, *Nannodectes gidleyi*, AMNH 17171 (Tiffanian); D, *Phenacolemur simonsi*, USGS 9620 (early Wasatchian); E, *Phenacolemur* cf. *pagei*, USGS 2216 (late Clarkforkian); F, *Phenacolemur* sp.,



In presumed paromomyid I's the anterocone and laterocone are typically well-developed and the posterocone is usually somewhat smaller, but the mediocone is quite variable. The mediocone is nearly as big and as distal as the anterocone in early Wasatchian *Phenacolemur simonsi* (Fig. 3D), but much smaller and slightly more proximal in Clarkforkian *P. pagei* (Fig. 3E). In both of these, a short crest ("mediocrista") curves proximolaterad from the mediocone. I' in middle Wasatchian *Phenacolemur* sp. (Fig. 3F) has only a slightly less curved mediocrista but no distinct mediocone. In contrast, the mediocone of *Arcius lapparenti* (Fig. 3G) is the most distal cusp and is only slightly smaller than the subequal anterocone and laterocone, giving the apex a broad, serrate margin. A mediocrista is present and the posterocone is very large. *A. rougieri* (Fig. 3H) differs markedly in having the anterocone decidedly the largest cusp, the laterocone conspicuously more proximal, and the mediocone and posterocone nearly absent; again a distinct mediocrista is present. The differences between the I's of the two *Arcius* species when compared with other plesiadapiforms raise the question whether these two species should be included in the same genus.

Isolated upper incisors from the Thanetian of Walbeck, Germany, have been attributed to *Saxonella crepaturae* (Fig. 3J; see Russell, 1964:plate 8, fig. 6d). They are very similar to those of *Phenacolemur* (which is not known from the site), but have slightly stronger laterocone and posterocone and a small cusplule present on the mediocrista. The close correspondence to paromomyid incisors suggests that Saxonellidae could be more closely related to Paromomyidae than to any other plesiadapiform family (see also Gingerich, 1976), although this is not particularly supported by other aspects of the dentition (Rose, 1975; Fox, 1991).

An associated I' of a carpolestid (*Carpolestes nigridentis*, the most derived and youngest species) has recently been illustrated (Gingerich, 1987:fig. 6) but not described. From the published figure it appears to differ from other plesiadapiforms (including putative carpolestid I's), but resembles *Tinimomys*, in lacking a laterocone. Isolated I's referred to *Carpodaptes cygneus* (Fig. 3K; see Krause, 1978), however, are distinctive in having a very strong laterocone, even larger than the anterocone, a low crest mesioproximal to the anterocone but no mediocone, and a double posterocone, the lateral cusp substantially larger. An isolated I' identified as ?*Carpodaptes hazelae* by Fox (1984:fig. 6), judging from his figure, is similar to I' of *C. cygneus* but higher crowned and appears to have a small mediocone.

Two other previously illustrated isolated incisors are of interest and might belong to carpolestids. A tiny I' (USNM 9928, Fig. 3L) from the middle Paleocene Gidley Quarry ascribed by Gidley (1923:plate 3, fig. 10) to cf. *Palaechthon minor* (= *Palenochtha minor*) is strongly suggestive of incisors of plesiadapiforms and resembles I's of paromomyids and plesiadapids in particular. Like those, it has

←

USGS 27405 (middle Wasatchian); G, *Arcius lapparenti*, AV 7714, medial and lingual views (Ypresian; after Godinot, 1984); H, *Arcius rougieri*, PAT 1 (Ypresian; after Godinot, 1984, and a cast of PAT 1); I, *Megadelphus lundeliusi*, AMNH 55284, lateral view (late Wasatchian; root restored from *Microsyops latidens*, USNM 19319; modified after Szalay, 1969a); J, *Saxonella crepaturae*, Wa/393 (Thanetian); K, *Carpodaptes cygneus*, UA 11088 (late Tiffanian); L, Unidentified incisor, probably either *Elphidotarsius florencae* or *Palenochtha minor*, USNM 9928 (Torrejonian); M, ?*Apatemys* sp., USGS 2460 (early Wasatchian). Scales are 1 mm.



a well-developed anterocone, laterocone, mediocone, and posterocone. The first three cusps are subequal in size. In addition, however, there is a small cuspule at the base of the mediocone ("medioconule") and a small but distinct lateroconule. The incisor is too small to belong to any known Gidley Quarry plesiadapiform besides *P. minor* or *Elphidotarsius florencae*. Although it is not possible at present to determine which (if either) of these species this incisor represents, the possibility that it may belong to *Elphidotarsius* should not be overlooked. Simpson (1928: fig. 13) depicted an incisor (AMNH 22169) from the Clarkforkian Bear Creek locality, which appears from his drawing to have a similar cusp arrangement, except for a double lateroconule. It is tempting to conclude that, if the Gidley Quarry incisor pertains to *Elphidotarsius*, the Bear Creek incisor could belong to the derived carpolestid *Carpolestes nigridentis*. However, both incisors are more elaborate than others that have been referred to carpolestids, and the Bear Creek specimen appears to differ significantly from the incisor of *Carpolestes nigridentis* illustrated by Gingerich (1987).

This raises the alternative that both of these incisors might instead belong to nonplesiadapiforms. The best candidates in that case are erinaceid or nyctitheriid insectivores, or plagiomenids, one or more of which are recorded from Gidley Quarry and Bear Creek, and all of which are known to have had multilobed lower incisors (e.g., Rose, 1973; Schwartz and Krishtalka, 1976; Sigé, 1976). Undescribed upper incisors from the Eocene of Ellesmere Island (in the Carnegie Museum collection), probably attributable to plagiomenids, closely resemble Simpson's Bear Creek incisor.

There is general agreement that the families discussed above are plesiadapiforms. More controversial is the Microsyopidae sensu stricto (i.e., not including Paleocene Palaechthonidae; see Gunnell, 1989). Since they have been considered plesiadapiforms by some workers (e.g., Bown and Rose, 1976; Gingerich, 1989; Gunnell, 1989), we include them here. Serially associated I's have been reported in early Bridgerian *Megadelphus lundeliusi* (Fig. 3I; see Szalay, 1969a:plates 50 and 52; Gunnell, 1989:fig. 49) and later Wasatchian *Microsyops latidentis* (Gunnell, 1989:fig. 36, 48). The latter specimen is damaged at the tip, and it is possible that it is I<sup>2</sup> rather than I<sup>1</sup>. Szalay (1969a:plate 36) also allocated an isolated incisor (USNM 19319) to *M. latidentis*. It is noteworthy that all of these incisors are simple, conical or laterally compressed, and caniniform. They are very different from the multicusped incisors of plesiadapiforms, including *Tinimomys*. This structure does not provide support for close relationship of Microsyopidae with any known plesiadapiforms.

The isolation of *Tinimomys* relative to other genera conventionally considered plesiadapiforms is enhanced by the structure of its I<sup>1</sup> (Fig. 3A). In contrast to other plesiadapiforms, the posterocone in *Tinimomys* is weaker, and there is no laterocone. Moreover, the crown of I<sup>1</sup> in *Tinimomys* is relatively shorter than in most other plesiadapiforms, and in lateral perspective the tooth is more hook-shaped. In this regard it is more like the I<sup>1</sup> that has been referred to *Microsyops* (e.g., Gingerich, 1976:fig. 38; Bown, 1979:fig. 44e) but which belongs to almost certainly *Apatemys* (Fig. 3M; see Gingerich and Rose, 1982:fig. 1B); however, there is little other specific resemblance to apatemyids.

Probably the closest similarity to I<sup>1</sup> of *Tinimomys* is seen in isolated incisors from Gidley Quarry (USNM 10010 and 10090, Fig. 3B) identified by Gidley (1923:plate 3, fig. 8–9) as cf. *Pronothodectes* species. Like I<sup>1</sup> of *Tinimomys*, these incisors have relatively short crowns, an indistinct posterocone, and apparently a basal lateroconule (somewhat larger than in *Tinimomys*), but no laterocone.



They are less hook-shaped and have larger, more apical mediocones than in *Tinimomys*. These teeth are structurally unlike plesiadapid incisors and are probably too small to represent *Pronothodectes* anyway. Their size is most appropriate to belong to either *Paromomys depressidens* or *Palaechthon alticuspis* among Gidley Quarry plesiadapiforms and, because they also differ markedly from known paromomyid incisors, it is probable that they represent *Palaechthon*. (It is also possible, but we think less likely, that they do not belong to a plesiadapiform.) If our assignment is correct, the resemblance between these incisors and those of *Tinimomys* could be interpreted as evidence of a closer relationship between micromomyids and palaechthonids than between micromomyids and any other plesiadapiform family. However, because these incisors are simpler than those of other plesiadapiforms, the similarities could be largely or entirely plesiomorphous, indicating only that both families branched early from the plesiadapiform stem and retained the primitive incisor form. In this regard it is notable that recently discovered postcranial specimens of *T. graybulliensis* show derived resemblances to paromomyids and suggest a close relationship between micromomyids and paromomyids (Beard, in press).

#### COMMENT ON BODY-WEIGHT ESTIMATES

Weight estimates for these tiny mammals vary considerably depending on the regression equation used and the set of mammals selected to construct the equations. Conroy (1987) employed regressions based on lower molar size and body weight in extant primates to derive a weight estimate for *Tinimomys graybulliensis*, but inadvertent use of  $M_1$  area rather than the natural logarithm of its area resulted in obvious overestimates of 81 g (prosimian equation) and 86 g (all-primate equation). Applying Conroy's equations to the measurements of  $M_1$  by Bown and Rose (1976) and Beard and Houde (1989) (which are in close agreement, with mean  $M_1$  areas of 1.07 and 1.10, and  $\ln M_1$  areas of 0.07 and 0.10, respectively) the estimated mean body weight for *Tinimomys* should have been 16–17 g (prosimian equation) or 14–15 g (all-primate equation), much smaller than any extant primate. The equation of Gingerich et al. (1982), derived from the relationship between  $M_1$  area and body mass in extant generalized primates, provides an estimate of 39–41 g. The same equations yield a weight of 21–23 g or 53 g, respectively, for the new specimen of *Tinimomys* described here. For the individual of *Niptomomys* described above we estimate the body weight to have been either 28–29 g or 68 g using these regressions.

As observed by Gingerich et al. (1982; see also Gingerich and Smith, 1984), living insectivores and insectivorous primates such as *Tarsius* have relatively large teeth compared to body mass and, therefore, smaller body weights than would be predicted using their generalized primate regression. In view of the dental anatomy of these two fossil genera (particularly *Tinimomys*) and their very small tooth size, their body weights were almost certainly at the lower end of the predictions above, and probably more consistent with those of insectivores than of primates. Living insectivores (soricids) with molar sizes comparable to *Tinimomys* typically weigh less than 10 g (see Gingerich and Smith, 1984:fig. 5).

#### ACKNOWLEDGMENTS

We thank T. M. Bown, R. J. Emry, R. C. Fox, P. D. Gingerich, M. Godinot, D. W. Krause, and D. E. Savage for access to specimens or casts and permission to illustrate specimens herein. We also thank T. M. Bown, G. F. Gunnell, D. W. Krause, and C. B. Ruff for discussion, and T. M. Bown and an anonymous reviewer for helpful comments on the manuscript. Elaine Kasmer prepared the illus-



trations. Field work leading to recovery of the *Tinimomys* specimen described here was supported by a Smithsonian Scholarly Studies Grant to PH. We gratefully acknowledge support from NSF grants BSR-8918755 (to KDR) and BSR-9020276 (to Carnegie Museum).

### LITERATURE CITED

- BEARD, K. C. 1990. Gliding behaviour and palaeoecology of the alleged primate family Paromomyidae (Mammalia, Dermoptera). *Nature*, 345:340–341.
- . 1991. Vertical postures and climbing in the morphotype of Primatomorpha: Implications for locomotor evolution in primate history. Pp. 79–87, in *Origine(s) de la Bipédie chez les Hominidés* (Y. Coppens and B. Senut, eds.), Editions du CNRS (Cahiers de Paléanthropologie), Paris.
- . 1993. Phylogenetic systematics of the Primatomorpha, with special reference to Dermoptera. Pp. 129–150, in *Mammal Phylogeny, Volume 2, Placentals* (F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds.), Springer-Verlag, New York.
- . In press. Origin and evolution of gliding in early Cenozoic Dermoptera (Mammalia, Primatomorpha). In *Primates and Their Relatives in Phylogenetic Perspective* (R. D. E. MacPhee, ed.), Plenum, New York.
- BEARD, K. C., AND P. HOUE. 1989. An unusual assemblage of diminutive plesiadapiforms (Mammalia, ?Primates) from the early Eocene of the Clark's Fork Basin, Wyoming. *Journal of Vertebrate Paleontology*, 9:388–399.
- BOWN, T. M. 1979. Geology and mammalian paleontology of the Sand Creek Facies, lower Willwood Formation (Lower Eocene), Washakie County, Wyoming. *Geological Survey of Wyoming Memoir* 2:1–151.
- BOWN, T. M., AND P. D. GINGERICH. 1972. Dentition of the early Eocene primates *Niptomomys* and *Absarokius*. *Postilla*, 158:1–10.
- BOWN, T. M., AND K. D. ROSE. 1976. New early Tertiary primates and a reappraisal of some Plesiadapiformes. *Folia Primatologica*, 26:109–138.
- CONROY, G. C. 1987. Problems of body-weight estimation in fossil primates. *International Journal of Primatology*, 8:115–137.
- FLEAGLE, J. G. 1988. *Primate Adaptation & Evolution*. Academic Press, New York, 486 pp.
- FOX, R. C. 1984. A new species of the Paleocene primate *Elphidotarsius* Gidley: Its stratigraphic position and evolutionary relationships. *Canadian Journal of Earth Sciences*, 21:1268–1277.
- . 1991. *Saxonella* (Plesiadapiformes: ?Primates) in North America: *S. naylori*, sp. nov., from the late Paleocene of Alberta, Canada. *Journal of Vertebrate Paleontology*, 11:334–349.
- GIDLEY, J. W. 1923. Paleocene primates of the Fort Union, with discussion of relationships of Eocene primates. *Proceedings of the U.S. National Museum*, 63:1–38.
- GINGERICH, P. D. 1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). *University of Michigan Papers on Paleontology*, 15:1–141.
- . 1987. Early Eocene bats (Mammalia, Chiroptera) and other vertebrates in freshwater limestones of the Willwood Formation, Clark's Fork Basin, Wyoming. *Contributions from the Museum of Paleontology, University of Michigan*, 27:275–320.
- . 1989. New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: Composition and diversity in a rarely sampled high-floodplain assemblage. *University of Michigan Papers on Paleontology*, 28:1–97.
- GINGERICH, P. D., AND K. KLITZ. 1985. Paleocene and early Eocene fossil localities in the Fort Union and Willwood formations, Clark's Fork Basin, Wyoming. *Miscellaneous Publications of the Museum of Paleontology, University of Michigan*:map.
- GINGERICH, P. D., AND K. D. ROSE. 1982. Studies on Paleocene and early Eocene Apatemyidae (Mammalia, Insectivora). I. Dentition of Clarkforkian *Labidolemur kayi*. *Contributions from the Museum of Paleontology, University of Michigan*, 26:49–55.
- GINGERICH, P. D., AND B. H. SMITH. 1984. Allometric scaling in the dentition of primates and insectivores. Pp. 257–272, in *Size and Scaling in Primate Biology* (W. L. Jungers, ed.), Plenum, New York.
- GINGERICH, P. D., P. HOUE, AND D. W. KRAUSE. 1983. A new earliest Tiffanian (late Paleocene) mammalian fauna from Bangtail Plateau, western Crazy Mountain Basin, Montana. *Journal of Paleontology*, 57:957–970.
- GINGERICH, P. D., B. H. SMITH, AND K. ROSENBERG. 1982. Allometric scaling in the dentition of primates and prediction of body weight from tooth size in fossils. *American Journal of Physical Anthropology*, 58:81–100.
- GODINOT, M. 1984. Un nouveau genre de Paromomyidae (Primates) de l'Éocène inférieur d'Europe. *Folia Primatologica*, 43:84–96.



- GUNNELL, G. F. 1989. Evolutionary history of Microsyopoidea (Mammalia, ?Primates) and the relationship between Plesiadapiformes and Primates. *University of Michigan Papers on Paleontology*, 27:1–157.
- HOFFSTETTER, R. 1988. Origine et évolution des primates non humains du nouveau monde. Pp. 133–170, in *L'Évolution dans sa réalité ses diverses modalités*. Colloque international (Paris 1985, Fondation Singer-Polignac), Masson, Paris.
- HOOKE, J. J. 1991. The sequence of mammals in the Thanetian and Ypresian of the London and Belgian basins. Location of the Palaeocene–Eocene boundary. *Newsletters on Stratigraphy*, 25: 75–90.
- HOUE, P., AND S. L. OLSON. 1992. A radiation of coly-like birds from the Eocene of North America (Aves: Sandcoleiformes new order). *Natural History Museum of Los Angeles County, Science Series*, 36:137–160.
- KAY, R. F., J. G. M. THEWISSEN, AND A. D. YODER. 1992. Cranial anatomy of *Ignacius graybullianus* and the affinities of the Plesiadapiformes. *American Journal of Physical Anthropology*, 89:477–498.
- KAY, R. F., R. W. THORINGTON, JR., AND P. HOUE. 1990. Eocene plesiadapiform shows affinities with flying lemurs not primates. *Nature*, 345:342–344.
- KRAUSE, D. W. 1978. Paleocene primates from western Canada. *Canadian Journal of Earth Sciences*, 15:1250–1271.
- MARTIN, R. D. 1986. Primates: A definition. Pp. 1–31, in *Major Topics in Primate and Human Evolution* (B. Wood, L. Martin, and P. Andrews, eds.), Cambridge University Press, Cambridge, 364 pp.
- . 1990. *Primate Origins and Evolution: A Phylogenetic Reconstruction*. Princeton University Press, Princeton, 804 pp.
- MATTHEW, W. D. 1917. The dentition of *Nothodectes*. *Bulletin of the American Museum of Natural History*, 37:831–839.
- McKENNA, M. C. 1960. Fossil Mammalia from the early Wasatchian Four Mile Fauna, Eocene of northwest Colorado. *University of California Publications in Geological Sciences*, 37:1–130.
- REPENNING, C. A. 1967. Subfamilies and genera of the Soricidae. *U.S. Geological Survey Professional Paper*, 565:1–74.
- ROSE, K. D. 1973. The mandibular dentition of *Plagiomene* (Dermoptera, Plagiomenidae). *Breviora*, 411:1–17.
- . 1975. The Carpolestidae, early Tertiary primates from North America. *Bulletin of the Museum of Comparative Zoology*, 147:1–74.
- . 1981. The Clarkforkian Land-mammal Age and mammalian faunal composition across the Paleocene–Eocene boundary. *University of Michigan Papers on Paleontology*, 26:1–197.
- ROSE, K. D., AND T. M. BOWN. 1982. New plesiadapiform primates from the Eocene of Wyoming and Montana. *Journal of Vertebrate Paleontology*, 2:63–69.
- RUSSELL, D. E. 1964. Les mammifères Paléocènes d'Europe. *Mémoires du Muséum National d'Histoire Naturelle, Série C*, 13:1–324.
- . 1967. Sur *Menatherium* et l'âge Paléocène du gisement de Menat (Puy-de-dôme). *Problèmes Actuels de Paléontologie, Colloques Internationaux du CNRS*, 163:483–490.
- SCHWARTZ, J. H., AND L. KRISHTALKA. 1976. The lower antemolar teeth of *Litolestes ignotus*, a late Paleocene erinaceid (Mammalia, Insectivora). *Annals of Carnegie Museum*, 46:1–6.
- SIGÉ, B. 1976. Insectivores primitifs de l'Éocène supérieur et Oligocène inférieur d'Europe occidentale. Nyctithériidés. *Mémoires du Muséum National d'Histoire Naturelle, Série C*, 34:1–140.
- SIMPSON, G. G. 1928. A new mammalian fauna from the Fort Union of southern Montana. *American Museum Novitates*, 297:1–15.
- . 1935. The Tiffany fauna, upper Paleocene. II.—Structure and relationships of *Plesiadapis*. *American Museum Novitates*, 816:1–30.
- SWINDLER, D. 1976. *Dentition of Living Primates*. Academic Press, New York, 308 pp.
- SZALAY, F. S. 1969a. Mixodectidae, Microsyopidae, and the insectivore–primate transition. *Bulletin of the American Museum of Natural History*, 140:193–330.
- . 1969b. Uintasoricinae, a new subfamily of early Tertiary mammals (?Primates). *American Museum Novitates*, 2363:1–36.
- . 1974. A new species and genus of early Eocene primate from North America. *Folia Primatologica*, 22:243–250.
- SZALAY, F. S., AND E. DELSON. 1979. *Evolutionary History of the Primates*. Academic Press, New York, 580 pp.